UPPER DEVONIAN TETRAPODS FROM ANDREYEVKA, TULA REGION, RUSSIA

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ABSTRACT. Devonian tetrapod remains have been recovered from the Famennian of Russia. They occurred in a limestone with stromatolites, algae, numerous and diverse fish remains and the holotype of the tetrapod *Tulerpeton curtum*. The conditions indicate a shallow-water basin with carbonate-rich water and perhaps an estuarine or marine situation. The individual bones show some plesiomorphic similarities to those of other Devonian tetrapods and osteolepiform fishes, such as a high premaxillary tooth count, large fangs plus a marginal row of smaller teeth on the vomer, a low naris with unsutured premaxillary–maxillary junction, lack of shagreen on the coronoids and lateral line canals in tubes through the bone, but also share derived characters with some Carboniferous tetrapods, such as shagreen on the vomer, shape and suture pattern of supratemporal and intertemporal, and possession of a tabular horn. The findings indicate that tetrapods were already diverse by the Devonian, and that they may not have been confined to freshwater.

THE earliest known tetrapods occur in Upper Devonian deposits, and have been described from East Greenland (Säve-Söderbergh 1932; Jarvik 1952, 1980; Clack 1988, 1989; Coates and Clack 1990, 1991), Australia (Warren and Wakefield 1972; Campbell and Bell 1977), Scotland (Ahlberg 1991) and Central Russia (Lebedev 1984, 1985, 1990). These fossils are of great importance in enhancing our understanding of the transition from fish to tetrapod and of the acquisition of the unique characters by which tetrapods are defined.

Tulerpeton curtum (Lebedev 1984, 1985, 1990) is one of only three Devonian tetrapods for which articulated material has been described. It consists of complete, articulated, right fore and hind limbs, in which the digits are preserved. Most of the left half of the shoulder girdle and part of the left pelvic girdle, some centra, ribs and articulated ventral scalation are preserved in association. The significance of *Tulerpeton* lies partly in its possession of six digits on the manus and probably six on the pes. Other known Devonian tetrapods also have more than five digits on each limb. *Acanthostega* (Coates and Clack 1990) has eight digits on the manus and *Ichthyostega* (Coates and Clack 1990) has seven digits on the pes. Together, these genera have contributed greatly to our understanding of the origin of tetrapod limbs (Coates and Clack 1990; Coates 1991; Gould 1991). The postcranial material of *Tulerpeton* is being described in detail by one of the current authors (O. A. L.) and M. I. Coates of the University of Cambridge, but this paper describes cranial material associated with the holotype specimen, and other cranial remains from the same horizon.

The holotype of *Tulerpeton curtum* and two associated cranial elements derive from a single block of limestone from the Andreyevka-2 locality in the Tula Region in Central Russia. The sedimentology and associated biota are interpreted as deriving from an environment similar to the Black Sea limans, essentially estuarine or brackish conditions with both freshwater sources and occasional marine incursions (Lebedev in press). Most tetrapod bones were found as isolated elements distributed through the horizon, as were those from placoderms (antiarchs), acanthodians, sarcopterygians (new species of osteolepiforms (to be described elsewhere), porolepiforms, struniiforms, dipnoans), and actinopterygians (palaeonisciforms), as well as ostracodes, worms, stromatolites and charophytes. Apart from the articulated *Tulerpeton* limbs, the bones are dissociated, but most can be readily identified as belonging to one or other of the fish groups. The tetrapod elements clearly do not belong to any of the known fish groups, and are identified as tetrapod on the basis of the shape and bone ornamentation. Initially these were all attributed to

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Tulerpeton curtum, as tetrapods are rare in the fauna and were assumed to be represented by a single taxon. Subsequently, at least two types of tabular have been identified, suggesting that other taxa may have been present. Therefore we must be cautious in attributing any material except that associated with the holotype, to *Tulerpeton*, though we believe this to be the most likely possibility for the majority.

Tulerpeton represents the first early tetrapod to be associated with an estuarine or occasionally marine environment. The remains exhibit marked differences from those of the other two described Devonian genera, and indicate that by the Famennian, diverse tetrapod morphologies and ecologies already existed.

MATERIAL AND METHODS

The material was collected during three trips in 1982–1983 by one of the authors (O.A.L.), who joined the field teams of the Palaeontological Institute of the Academy of Sciences. The locality was discovered by M. F. Ivakhnenko. The material is stored in the Palaeontological Institute of the Academy of Sciences, Moscow (PIN), collection number PIN 2921. The premaxilla (PIN 2921/8) and vomer (PIN 2921/9), still in sutural attachment, were found with the holotype postcranial material and are attributed to it. Other isolated elements cannot be safely attributed at this stage. Other material discussed is in the Natural History Museum, London (BMNH), National Museum of Scotland, Edinburgh (NMS), Geological Museum, Copenhagen (MGUH).

Most of the cranial elements were found following acid digestion of rock from the fossiliferous layer, and are listed below: a premaxillary (PIN 2921/35); two incomplete jugals (PIN 2921/36, 37); two postfrontals (PIN 2921/41, 457), one of the postfrontals fitting onto a parietal (PIN 2921/457), two further parietals (PIN 2921/38, 3014); a postorbital (PIN 2921/3002); an intertemporal (PIN 2921/3003); two supratemporals (PIN 2921/39, 40); three tabulars (PIN 2921/42, 447, 458); a dentary (PIN 2921/32); a coronoid (PIN 2921/33); two angulars (PIN 2921/31, 446). Other fragments include part of a maxilla (PIN 2921/34), and part of a possible further tabular (PIN 2921/1000), but they are either too incomplete or too uncertainly identified to warrant description here. Pencil specimen drawings were made by one of the authors (O.A.L.) using a binocular microscope MBS-1 with a grid inserted into one of the eye-pieces. These were then redrawn in Chinese ink.

STRATIGRAPHY, SEDIMENTOLOGY AND TAPHONOMY

The Andreyevka-2 locality is situated on the Tresna River, 300 m upstream from Andreyevka village (Suvorov District, Tula Region, Russia). A small outcrop of Khovanshchina beds (Zavolzhsky horizon, Famennian, Upper Devonian), surrounded by Carboniferous strata, has been exposed by erosion on the right bank near water level. Dating was made on the basis of the presence of *Eusthenodon* sp. nov., also found in the Khovanshchina beds of the Draguny locality on the Plava River (South of the Tula Region). The ostracodes from Andreyevka-2 were determined as being of Khovanshchina age (Fa 2d – Tn 1a of the French–Belgian Basin) (V. A. Chizhova, personal communication) and include the following taxa: *Aparchites globulus*, *Bykavites nativus*, *Evlanella sokolovi*, *Glyptolichwinella* cf. *G. spiralis*, *Healdianella punctata*, *Aparchitellina* sp., *Carbonita* sp. The lowermost bed is a limestone containing isolated bones and scales of *Holoptychius* cf. *H. nobilissimus* and a new osteolepidid. It is overlain by an almost continuous stromatolite layer. Above that lie limestones containing articulated *Remigolepis armata* and *Bothriolepis* carapaces, isolated sarcopterygian bones, and the remains of *Tulerpeton curtum*.

The overlying layer is a bone bed about 100 mm thick, filled with bones, scales and teeth of many taxa: Antiarchi: *Remigolepis armata*; Sarcoptergyii; *Eusthenodon* sp. nov., Osteolepididae gen. et sp. nov., *Strunius* sp.; Dipnoi; *Andreyevichthys epitomus*; Chondrichthyi fam., gen. et sp. nov.; Acanthodii; *Devononchus concinnus*, *D. laevis*, '*Cheiracanthus*' sp.; Palaeonisci; *Moythomasia* sp.

Invertebrates are represented by very thin-shelled, undeterminable bivalves, and tubes of the sedentary worm *Serpula vipera*, abundant on the upper surfaces of stromatolites and penetrating them. Gyragonites and stem-cores of charophyte algae may belong to the genus *Quasiumbella*. The upper part of the section consists of intercalated limestones and clays, containing a few detached scales and bones of fishes (Lebedev 1986).

The sedimentary environment was probably a quiet shallow basin, of warm, possibly marine or brackish water, containing a high percentage of dissolved carbonates and clay particles (Lebedev in press).

Most of the bones are well preserved and unworn, but, with a few exceptions such as the material of *Tulerpeton*, completely disarticulated. Coarse-grained material is almost absent, suggesting still water conditions. The bones appear to show no current sorting nor preferred orientation, but as most of the specimens have been recovered by acid digestion, this must be judged on a partial sample.

The removal of most of the head and the left part of the body and tail, while the right side and the scale cover remain in articulation, suggests postmortem disruption of the body by decay gases rather than scavenging. The mass death of fishes and tetrapods seen in the upper fossiliferous layers may result from the basin having dried up at some stage. There was almost no water transportation and subaqueous maceration was fast and efficient.

DESCRIPTION

Cranial material of Tulerpeton curtum

Premaxilla. The premaxilla is sutured to the vomer (Text-fig. 1A–D), allowing both to be oriented with respect to the midline. The whole unit (PIN 2921/8, 9) can usefully be compared with those of other early tetrapods and sarcopterygian [osteolepiform] fishes, in particular, the contemporary *Ichthyostega* (Jarvik 1980) and *Acanthostega* currently under study by one of us (J.A.C.).

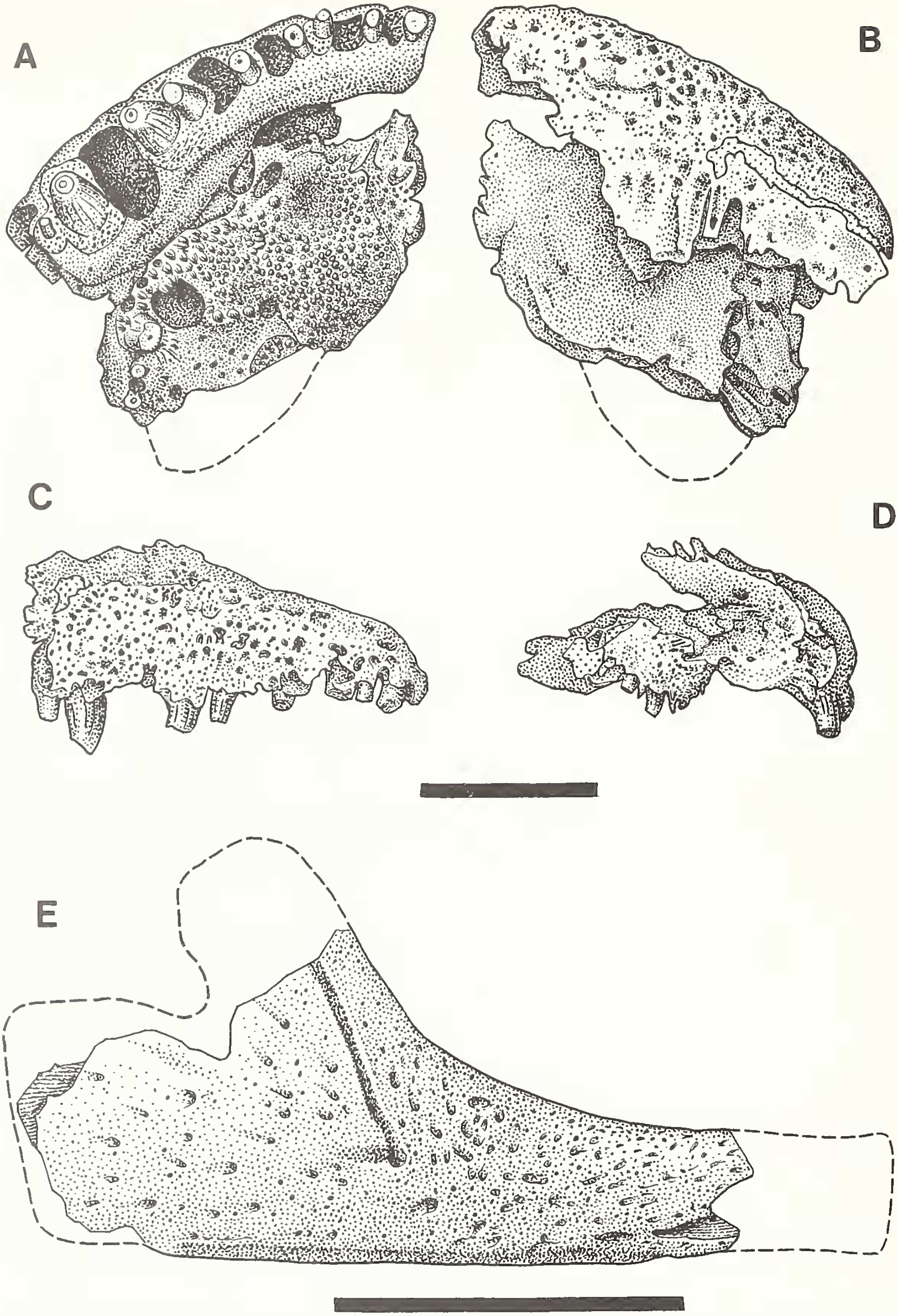
The premaxilla bears characteristically tetrapod-like ornament consisting of irregular pits and ridges (Text-fig. 1B–C). It is slightly wider than long and deeper medially than laterally, with a short symphysial region. Its shape indicates an animal with a broad, low snout, which is more characteristic of early tetrapods than of any of the contemporary fishes except *Panderichthys* and *Elpistostege* (Worobyeva 1973; Vorobyeva 1977, 1980; Schultz and Arsenault 1985). A wide, short process meets the nasal; the contact is almost transverse to the midline (Text-fig. 1B). Medially, there is an embayment probably for paired or a single internasal like those found in loxommatids (Beaumont 1977) and *Acanthostega* (Clack 1989) or a fontanelle like that in *Crassigyrinus* (Panchen 1985), chroniosuchids (Ivakhnenko and Tverdokhlebova 1980) and zatrachidids (Langston 1953). There is no notch for the external naris nor a sutural surface for contact with the maxilla. Thus there may only have been a ligamentous junction between these bones, as is probable in *Proterogyrinus* (Holmes 1984) and *Acanthostega*.

The palatal lamina of the premaxilla forms the anterior margin of a narrow, bean-shaped anterior palatal fossa, which tapers to a point towards the posterior part of the bone. The lamina expands here to meet the lateral margin of the vomer. The edge is gently curved; the fossa is prolonged postero-laterally by a gradually tapering fissure to the level of the middle of the palatal lamina of the premaxilla, as in *Acanthostega*.

Anterior palatal fossae (or fenestrae) are present in all known osteolepiform fishes such as *Eusthenopteron* (Jarvik 1980), such porolepiforms as *Glyptolepis* (Jarvik 1980), and in several primitive tetrapods such as *Ichthyostega* (Jarvik 1980), loxommatids (Beaumont 1977), *Crassigyrinus* (Panchen 1985) and *Greererpeton* (Smithson 1982). In the latter and in *Acanthostega*, the fossae are paired, separated by a process from the vomers. As in the latter, it is unclear whether the premaxilla contributed to the margin of the choana, though if it did, the contribution can only have been minimal.

The sensory canal enters the bone at the mid-point of the suture with the nasal and passes anterolaterally, branching to the surface with nine funnel-shaped foramina, only slightly larger than those found in the dermal ornament. Its posterior outlet lies dorsolateral to the base of the posterior tooth. Several sensory canal foramina are found on the lateral surface, joining the main sensory canal. The sensory line also lies within the bone in *Acanthostega* and *Greererpeton*, where a similar pattern of pores is seen. In contrast in *Crassigyrinus* and other early tetrapods, the premaxillary portion of the infraorbital canal lies in an open sulcus.

PIN 2921/35 is a fragment from the posterior part of a premaxilla. It is similar in general outline to PIN 2921/8 except that the postero-lateral edge of the palatal lamina is much more strongly curved, perhaps indicating a shorter snout and more transversely orientated apical fossa. In PIN 2921/8 the large posterior teeth are bordered laterally by a ridge, while in PIN 2921/35 the ridge is absent and the teeth are situated



TEXT-FIG. 1. A–D, *Tulerpeton curtum* Lebedev; Andreyevka; Famennian; PIN 2921/8, 9, right premaxilla and vomer in (A) ventral, (B) dorsal, (C) anterior and (D) posterior views; E, undetermined tetrapod, composite left jugal based on PIN 2921/36, 37, in lateral view. Scale-bars represent 10 mm.

immediately at the edge of the apical fossa. The most striking difference is the type of dermal ornament. In PIN 2921/35, small pits lie on a generally smooth surface, bearing occasional vascular pores, but in PIN 2921/8, the pits are funnel-shaped, separated by gentle ridges rather than flat surfaces.

There are fourteen teeth on premaxilla PIN 2921/8, their size gradually increasing caudally with the exception of the last, which is much smaller. The teeth are long and conical, their apices being strongly curved posteromedially. Longitudinal grooves at their base merge into fine striations apically, typical of labyrinthodont teeth.

A transverse section of the first premaxillary tooth (PIN 2921/8a) showed polyplocodont folding (Schultze 1969), in which the bone does not enter between dentine folds. The median line of the fold is straight, with neither meanders nor branches. There are no dentine zones such as those in *Panderichthys* (Schultze 1969). The pattern is most similar to that in *Megalichthys*. In *Tulerpeton*, the folds are closely appressed, with the bone excluded from between them. It is characteristic of most early tetrapod tooth folding that the fold-line meanders. It is possible that a section through a vomerine tusk (standardly used for cross-sections by Schultze and others, for example Atthey (1876; Embleton and Atthey 1874)) rather than a premaxillary tooth would show this more complex pattern. It is also possible that this tooth pattern is genuinely more primitive and fish-like. 'Dark dentine' (Panchen 1985) is absent.

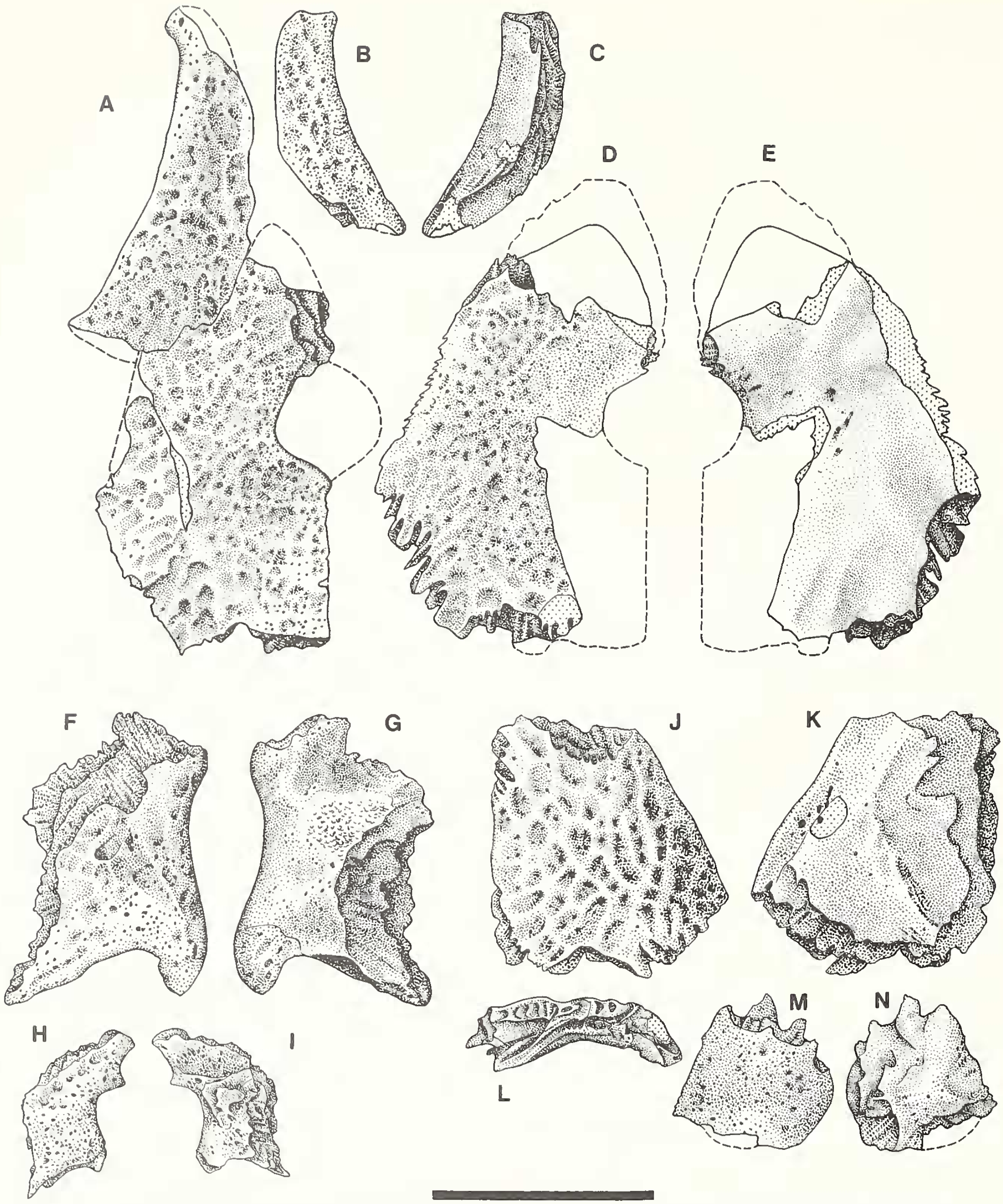
Vomer. The vomer (PIN 2921/9) (Text-fig. 1A) is diamond-shaped, almost flat and shagreen-covered, except for a triangular area posteriorly. This region is pierced by several large vascular foramina and bordered anteriorly and laterally by a row of denticles larger than those of the shagreen field. These lie on a curved ridge bearing a series of teeth, including a fang and replacement pit, and three smaller teeth. The ridge borders the choana anteromesially. The anteromedial corner of the vomer lacks shagreen but bears a network of large vascular foramina. A rugose longitudinal projection lies along the medial suture, which may indicate the presence of a cartilage-covered pad which may have acted as a shock-absorber during jaw closure, preventing possible injury to the vomer caused by the tips of dentary tusks. In *Ichthyostega*, there is a boss in the same position. Laterally a depression perhaps accommodated an adsymphysial tusk of the lower jaw. A slightly smaller pit is situated at the base of a vertical ridge which runs parallel to the sutural area with premaxilla.

Most of the dorsal (internal) surface of the vomer is smooth and only the posterolateral portion, which slopes gently down to the edge of choana, is rugose and pierced by numerous vascular foramina. This area is sharply demarcated from the rest of the dorsal surface by a distinct angle. It marks the anterior limit of the nasal capsule and corresponds to a similar tuberous, pore-bearing area on the dorsal side of the ventral lamina of premaxilla. Anterolateral to the tooth-bearing ridge, the vomer is produced into a lamina which forms a tongue and groove contact with the premaxilla.

Among tetrapods, the pattern of dentition on the premaxilla and vomer is closely matched by, but is clearly different from, that of *Acanthostega*. In that genus, there are thirteen premaxillary teeth, with a similar size distribution to that of this premaxilla. *Greererpeton* possesses a similar distribution and number, but there is relatively less variation among all except the last three teeth. *Greererpeton* has a very small posteriormost tooth, preceded by two which are enlarged into fangs comparable in size to those on the palate. *Ichthyostega* has fewer premaxillary teeth (nine), with little size variation along the row. The tooth distribution of this premaxilla resembles those of other early tetrapods more closely than it does those of osteolepiforms such as *Eusthenopteron* and the osteolepidids; *Panderichthys rhombolepis* has about twenty small teeth on either side of the jaw; their size distribution varies in different individuals. In some respects, the premaxillae PIN 2921/8, 35 are similar to that of a newly recognized Devonian tetrapod (PIN 54/180c) from Latvia, previously attributed to *Panderichthys bystrowi* Gross (Vorobyeva 1962; Ahlberg 1991), which is being described by Drs P. Ahlberg, E. Luksevics and one of us (O.A.L.)

Like the premaxillary dentition, that of the vomer is most similar to *Acanthostega* among tetrapods, but differs in two respects. It has an expanded lamina anteriorly, bearing shagreen. This character is typical of most other early tetrapods; in lacking this lamina, *Acanthostega* resembles osteolepiform fishes. In most other tetrapod vomers, however, a large part of the shagreen field lies level with or posterior to the vomerine teeth. The palatal specimen attributed to *Crassigyrinus* (BMNH 30532) by Panchen (1985), appears to have been misinterpreted. It is currently under study by one of us (J.A.C.), but preliminary investigations show the vomer to lack a shagreen field and to have a tooth distribution similar to that of *Acanthostega* and PIN 2921/9. Vomers are unknown in the early anthracosaurs *Eoherpeton* (Smithson 1985) and *Proterogyrinus* (Holmes 1984), however, broad vomers associated with broad flat heads seem to be characteristic of the majority of early tetrapods.

The second difference between the vomer of PIN 2921/9 and that of *Acanthostega* lies in the position of the fang pair. In *Acanthostega*, the fang pair lies mesial to a curved tooth-bearing ridge as in osteolepiforms,



TEXT-FIG. 2. Undetermined tetrapod, cranial elements; Andreyevka; Famennian; A, PIN 2921/457, left postfrontal and parietal in dorsal view; B–C, PIN 2921/41, right postfrontal in dorsal and ventral views; D–E, PIN 2921/38, left parietal in dorsal and ventral views; F–G, PIN 2921/458, right tabular in dorsal and ventral views; H–I, PIN 2921/42, right tabular in dorsal and ventral views; J–L, PIN 2921/39, right supratemporal in dorsal, ventral and posterior views; M–N, PIN 2921/40, left supratemporal in dorsal and ventral views. Scale-bar represents 10 mm.

whereas in PIN 2921/9, the posterior fang lies more or less within the tooth-bearing ridge. The anterior replacement pit however, lies mesial to the tooth bearing ridge. In *Ichthyostega* the vomerine tusk pair, or rather slightly enlarged teeth are found at the beginning of the tooth row, followed by four or five smaller teeth (personal observation, O.A.L., J.A.C.).

Most early tetrapods have only a few teeth on the vomers, usually not more than a pair or, in some cases, clumps of small teeth. A fang pair plus a curving ridge bearing a row of smaller teeth and denticles is characteristic of many sarcopterygian fishes, and the distribution of teeth on this premaxilla and that of *Acanthostega* is the same as that found in *Eusthenopteron* and *Panderichthys*. *Ichthyostega* is intermediate between *Acanthostega* and PIN 2921/9 in the number of vomerine teeth, but it lacks shagreen. Some advanced temnospondyls, such as capitosaurs, also show a fang pair and a row of smaller teeth on the vomer (Bystrow and Efremov 1940), superficially like that of Devonian tetrapods. However, the relationship of the tooth row to the choana is different, and the row of teeth is continuous, rather than having the fang pair displaced from the row of small teeth. The condition is presumably convergent.

Undetermined cranial material

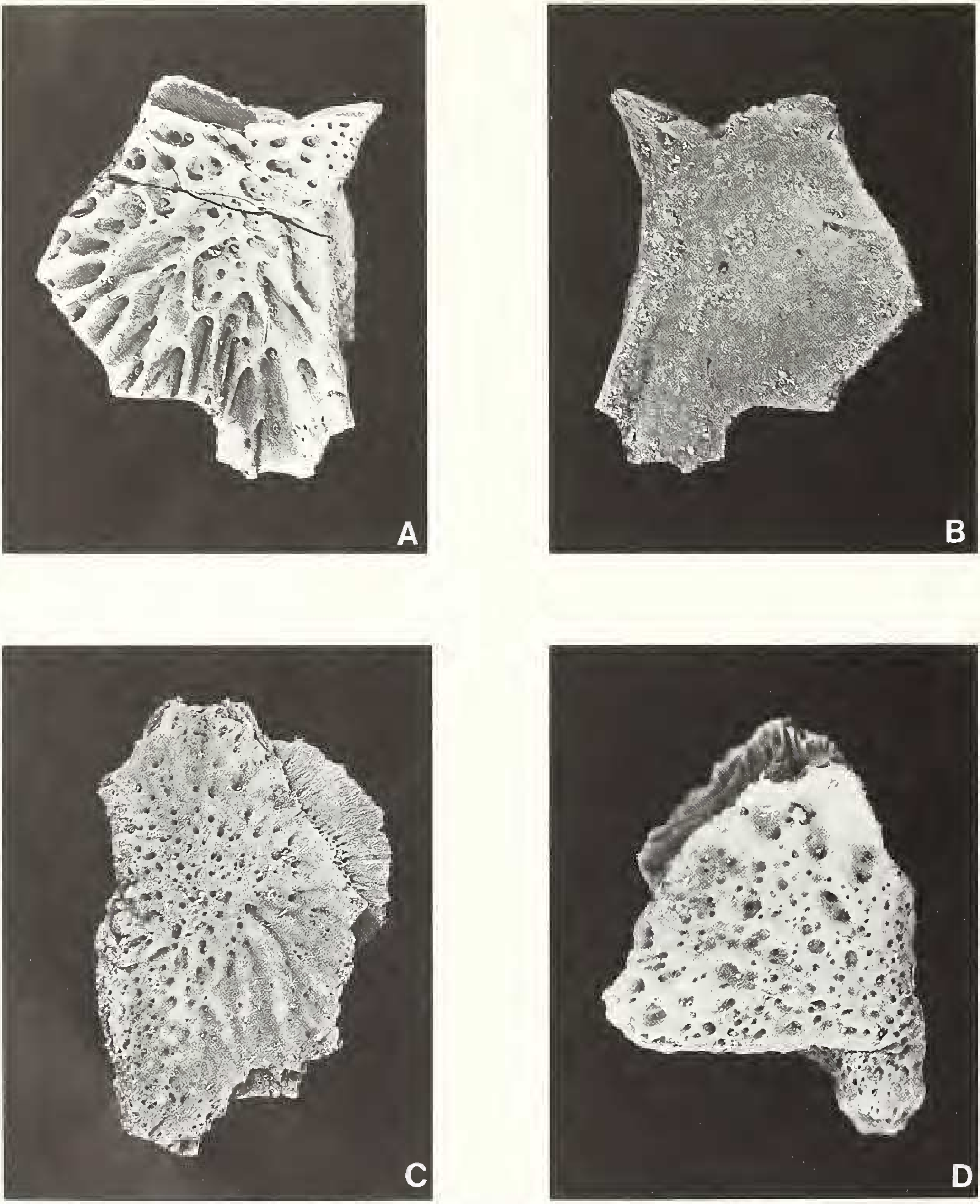
Jugal. The jugal is represented by two partial specimens from the right side, which together give an almost complete picture of the bone (PIN 2921/36, 37) (Text-fig. 1E). The suborbital process is low and long, and the postorbital lamina high; the orbit margin is a gentle curve, suggesting a relatively large orbit. The general shape of the bone is similar to the pattern found in *Proterogyrinus*, with a long, low suborbital region, and a deep notch for suture with the squamosal. The maxillary articulating surface is almost horizontal and slightly roughened; there is a poorly developed processus alaris. Like the jugal of *Acanthostega*, this bone shows a combination of lateral-line pores and a groove, with the jugal sensory line opening to the surface by a row of ovoid pores, and the postorbital commissure running in an open, although deep groove.

Postfrontal. The postfrontal is a long crescentic element (PIN 2921/41, 457) (Text-fig. 2A–C). Ventrally, the smooth surface is excavated so that while the lateral margin is thin, the bone thickens mesially to form a ridge along the suture with the parietal and frontal. In this respect and in its general proportions and shape it most closely resembles those of embolomeres such as *Pholiderpeton* (Clack 1987). Entry and exit foramina suggest the possible presence of an internal sensory canal, but no pores can be observed on the surface of the bone.

Parietal. The parietal is known from three specimens, one in sutural attachment with its postfrontal (PIN 2921/457) (Text-fig. 2A), a second isolated and somewhat broken example (PIN 2921/38) (Text-fig 2D–E) and a third very small specimen (PIN 2921/3014). PIN 2921/457 shows irregular pit and ridge ornament. The base of each pit is pierced by 1–3 foramina for blood vessels. The ornament of PIN 2921/38 is similar, though the pits are shallower, and there are no radiating grooves at the margins, which are almost smooth. The pineal foramen is large, and somewhat anteriorly placed. The edge of the pineal foramen is significantly raised, and lacks the usual pit and ridge ornament in PIN 2921/38 and bears only tiny vascular foramina, or small round pits. PIN 2921/457 bears depressions laterally and anterolaterally to the pineal foramen, resembling *Pteroplax cornutus* (Panchen 1970) in this respect. The parietal contacts (PIN 2921/38, 457 Text-fig. 2A, D–E) with postfrontal, intertemporal, supratemporal and postparietal are almost equal in length and straight, with no embayment for the supratemporal. The interparietal suture anterior to the pineal opening is complicated, with an overlapping surface.

PIN 2921/3014 is only about 7 mm in length and the ornament is very poorly developed, consisting only of small pits in the centre and radiating grooves laterally. It probably represents a very young individual.

Postorbital. The postorbital (PIN 2921/3002) (Text-fig. 3A–B), lacking only its posterior corner, is a plate-like triangular bone of a rather simple construction. The anterior margin, representing the posterior edge of the orbit, is slightly thickened dorsally at the area of a contact with the postfrontal. This contact is a simple smooth surface, bearing several vascular pores posteriorly and two larger foramina anteriorly, but neither rugosity, nor sutural sculpturing is evident. Ventrally the bone and corresponding orbital margin become thinner towards the overlap area with the jugal. Where the postfrontal and the intertemporal meet, the surface is marked by the opening of a rather large canal, perhaps representing the postorbital commissure of the lateral line canal. The contact area with the intertemporal is a shelf, bearing two rows of vascular pores on its lateral surface; the mesial surface is represented by a smooth narrow plate that appears to indicate kinetic attachment of skull roof and cheek as found in anthracosaurs. In *Crassigyrinus*, a similar plate constitutes the dorsal margin of the squamosal contacting the intertemporal posterior to the postorbital, seen in the holotype specimen NMS



TEXT-FIG. 3. Undetermined tetrapod, cranial elements; Andreyevka; Famennian; A–B, PIN 2921/3002, right postorbital in dorsal and ventral views, × 4; C, PIN 2921/3003, left intertemporal in dorsal view, × 4; D, PIN 2921/447, right tabular in dorsal view, × 10.

G.1859.33.104. The dermal ornament consists of small pits concentrated in the antero-dorsal corner, with grooves and ridges directed in a fan-shaped manner posteriorly and ventrally. The medial surface is smooth except for a narrow groove running parallel to the orbit margin and to a groove-like depression on the lateral surface parallel to the orbit margin.

Intertemporal. The outline of the intertemporal (PIN 2921/3003) (Text-fig. 3C) is similar to that in *Crassigyrinus* (Panchen 1985), '*Eogyrinus*' (Panchen 1972*a*; = *Pholiderpeton*, Clack 1987), *Proterogyrinus* (Holmes 1984) and *Archeria* (Holmes 1989). It is a roughly oval-trapezoid bone, its medial margin almost straight except for a small angle at about the mid-point. Here the sutural surface changes from a dorsally oriented anterior portion, to a more ventrally oriented posterior portion. The posterior margin bears an overlap for the supratemporal. The anterior margin shows a sutural notch, probably for the posterior corner of the postfrontal. The lateral margin, although partly broken off, is clearly sutureless; parallel to it runs a groove, rugose posteriorly, and an acute ridge. The groove and ridge might indicate continuation of the kinetic margin along the intertemporal as in *Crassigyrinus*. The ventral surface bears a central depression and several vascular foramina, possibly marking the anterior part of the roof of the adductor chamber. The ornament of most of the dorsal surface consists of a network of ridges with pits, more elongated towards the margins, between them.

Supratemporal. The supratemporal is an approximately pentagonal bone and is represented by two specimens of different sizes (PIN 2921/39, 40; Text-fig. 2J–N). The smaller specimen may represent a younger ontogenetic stage; it is generally similar to the larger specimen, but with its features in a less well developed form, for example, in dermal ornament. That of the smaller consists of numerous vascular pores; pits are present only at the periphery of the bone and are not as conspicuous as those on the larger element. The lateral margin is straight and lacks the interdigitations of a conventional sutural contact. This, like the matching margin of the postorbital and intertemporal, may be evidence of a 'kinetic' junction between the cheek and skull table, as in *Pteroplax cornutus*, which looks very similar (Clack 1987; O.A.L. personal observation). The contact for the intertemporal is oblique and arch-shaped. The parietal suture is long and almost straight. The posterior margin consists of two sutural facets: a lateral one for the tabular, occupying more than half of the total length, and a relatively short mesial facet for the postparietal. The implication is that there was no tabular–parietal contact as in anthracosaurs, but that the primitive condition of postparietal–supratemporal contact was retained. The ventral surface bears two depressions medially, an anterior and a posterior one, separated by a short ridge. The surface of the posterior depression is smooth and that of the anteromedial one bears slightly developed radial ridges and rugosities. The posterior depression may represent part of the roof of a spiracular chamber or its homologue, and the anteromedial one part of the roof of the adductor chamber.

Tabulars. Two elements are clearly identified as tabulars, PIN 2921/458 (Text-fig. 2F–G), PIN 2921/447, (Text-fig. 3D). The tabular PIN 2921/458 bears a small 'horn', like those of many early tetrapods, such as loxommatids, *Crassigyrinus* and *Proterogyrinus*. It is smooth and covered by vascular pores dorsally and rugose ventrally. The rugosity suggests the attachment of ligaments, probably running between the tabular and the shoulder girdle. The supratemporal suture is oblique and the contact area is wide; that for the postparietal is somewhat shorter and a little embayed for a lateral process from the postparietal. The edge bordering the temporal notch is gently curved. The mesial corner is produced farther posteriorly than the tabular horn. The posterior edge is not thickened, and lacks the occipital flange characteristic of anthracosaurs, though it would form a similar profile to their characteristic 'widow's peak'. Ventrally, a single large unfinished area, on a raised boss, indicates the attachment facet for the paroccipital process. The condition is most similar to that in loxommatids (Beaumont 1977 and personal observation O.A.L., J.A.C.), where a single facet is also found anteriorly placed on the bone. The dermal skull roof must have overhung the occipital face of the braincase to a significant degree. Double paroccipital facets are found on the tabulars of *Crassigyrinus*, as in anthracosaurs. In its relatively anterior position, the facet on this bone is most similar to the more anterior of these, but it is not possible to be sure to which it is really homologous.

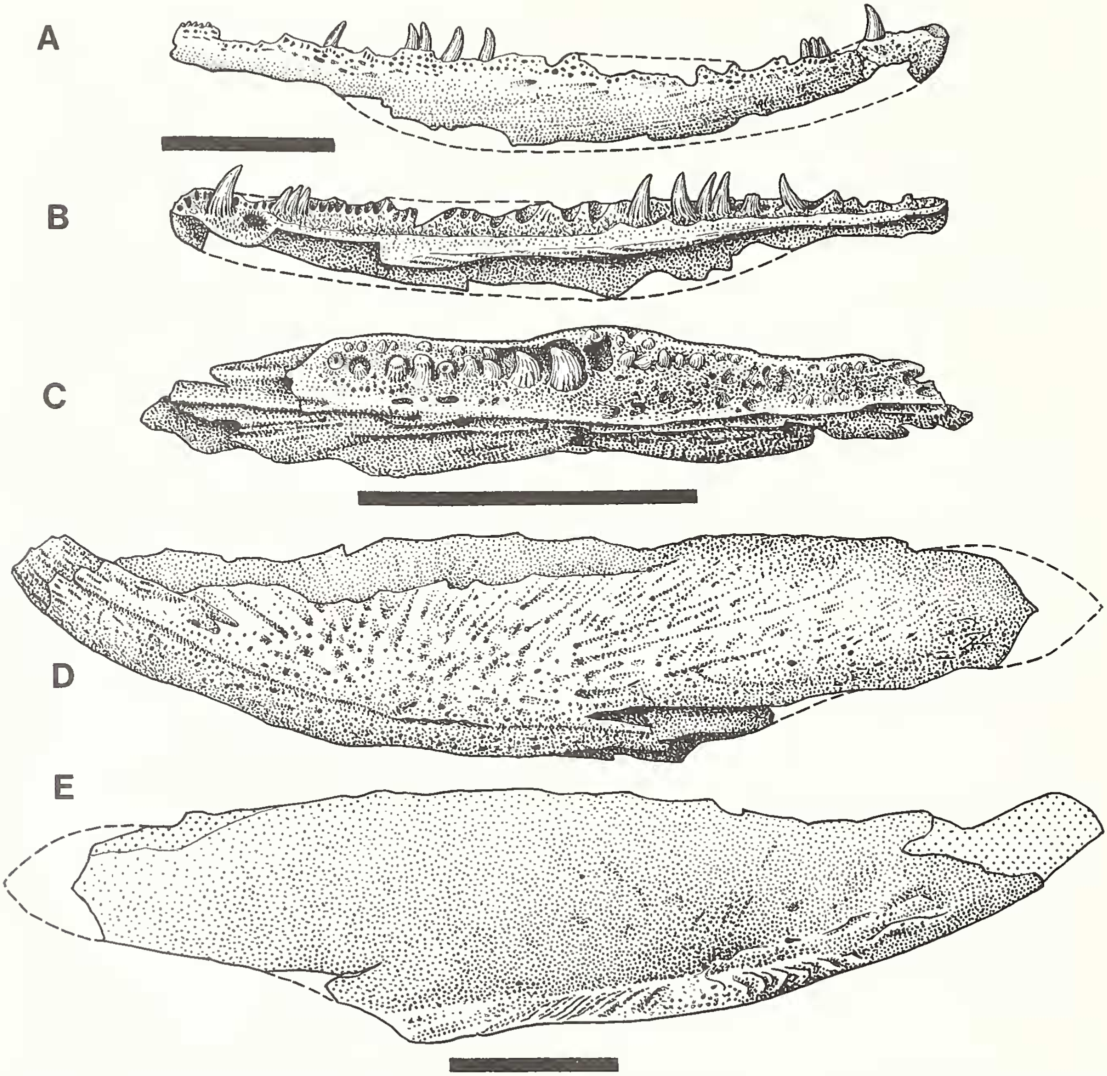
The tabular specimen PIN 2921/447 is generally similar to PIN 2921/458, but is much smaller. It probably represents a younger individual, but it may derive from a different species. It differs from PIN 2921/458 in the following respects. The bone is proportionately shorter and broader, and the horn is relatively larger and more massive. The posterior margin of the ornamented surface is straight and the free lateral margin not embayed. An oblique suture on the lateral margin may be for a narrow process of the supratemporal or for a process of the squamosal, as, for example, in *Loxomma acutirhinus* (Beaumont 1977, fig. 2*a*). On the ventral surface, there is no facet for the opisthotic.

PIN 2921/42 (Text-fig. 2H–I) is also identified as a tabular, though it is in some respects unusual. It has similar features to PIN 2921/458, including the presence of the opisthotic facet on the ventral surface and a small tabular horn. The margin of the temporal notch is much more strongly curved laterally, so that the tabular would have contributed to the anterior as well as the dorsal margin of the temporal notch. The lateral margin of this process bears an oblique suture, presumably for the squamosal, and in this feature, resembles

PIN 2921/447. If correctly identified, this feature would indicate that the skull/cheek contact was a firm suture, rather than a 'kinetic' one, and thus the element probably belongs to a separate taxon.

Lower jaw

Dentary. There are at least sixty marginal teeth on the dentary, their size gradually increasing caudally and reaching a maximum at the beginning of the posterior third of the dentary, decreasing thereafter. The lateral surface of the dentary (PIN 2921/32; Text-fig. 4A–B) is pierced by blood-vessel pores. These, situated at the bottoms of pits, are dispersed along the entire marginal tooth row at the uppermost margin of the bone. The lower part of the lateral surface is smooth, but bears occasional longitudinal grooves. The height of the vertical lamina decreases posteriorly to about a third of its maximum. The bone is enlarged anteriorly and forms a



TEXT-FIG. 4. Undetermined tetrapod, cranial elements; Andreyevka; Famennian; A–B, PIN 2921/32, right dentary in lateral and medial views; C, PIN 2921/33, left coronoid in dorsomedial view; D–E, PIN 2921/31, right angular in lateral and medial views. Scale bar represents 10 mm.

horizontal symphysial lamina which bears a pair of fangs, larger than the marginal teeth. Teeth in this position are also found in *Acanthostega*, *Ichthyostega* (Jarvik 1980), and apparently in *Proterogyrinus* (Holmes 1984), where they are also significantly larger than the marginal teeth. There is a rugose area on the lateral surface of the vertical lamina ventral to the symphysial plate. This area could be of perichondral or ligamentous origin and probably served as the attachment point for the lower jaw rami by a mentomandibular cartilage or short ligaments.

Coronoid. One coronoid is represented in the collection (PIN 2921/33; Text-fig. 4C). It is unlikely to be a posterior coronoid, since there is no adductor fossa notch posteriorly and each of the four sides is bounded by a sutural surface. Two rows of coronoid teeth are present; a lateral row of small teeth on the low vertical coronoid lamina as in osteolepiforms (for example, *Eusthenopteron* (Jarvik 1980), *Chrysolepis* (Lebedev, 1983), *Panderichthys rhombolepis* (Gross 1941), and *Holoptychius* (Jarvik 1980), and a medial row of larger teeth of which those in the centre are the largest. The structure and dentition of this bone is different from those of both other tetrapods and of most sarcopterygian fishes (i.e. excluding dipnoans). In fishes, the medial row of teeth consists of only a fang pair, to which the largest teeth in the row of PIN 2921/33 may be homologous. In *Ichthyostega* and the tetrapod *Doragnathus woodi* (possibly a juvenile *Spathicephalus*) (Smithson 1980*a*, 1980*b*) th adsymphysial plate and the coronoids bear a vertical lamina with a single row of teeth; there are the gaps in the tooth row between the coronoids in *Doragnathus*. In *Crassigyrinus*, fangs are situated within the main tooth row. Most other tetrapods bear shagreen on the coronoids, but may also bear teeth, usually quite small and irregularly arranged on the shagreen field. It is not clear to which row of teeth of Devonian tetrapods or sarcopterygians those of later tetrapods may be homologous.

Angular. Isolated angulars show the posteroventral margin (PIN 2921/31, 446) (Text-fig. 4D–E) to be a shallow curve, the length being more than four times the height. The lateral lamina reaches its maximum curve in the middle of the bone. The ornament consists of deep pits in the centre of the bone; dorsally and anteriorly they turn into deep grooves that diverge and become shallow and numerous. The mandibular sensory canal was housed in a deep groove in PIN 2921/31, like that in most other tetrapods, rather than in a canal as in *Acanthostega* and *Ichthyostega*. In PIN 2921/446 however, the central part is enclosed within the bone, as it is in a specimen from Celsius Bjerg, Greenland collected in 1947 (MGUH A88) (figured by Clack 1988, text-fig. 8 as a 'new taxon'). As in *Crassigyrinus*, there is a zig-zag suture with the postsplenial ventrally, where the lateral line groove is carried forward on a process of the angular before it passes onto the postsplenial. The mesial lamina is very narrow and bears a notch for a small Meckelian foramen, situated towards the middle third of the bone.

DISCUSSION

This material demonstrates a number of characters in which it is most closely comparable with the other Devonian tetrapods, *Acanthostega*, and *Ichthyostega*, and others in which it resembles post-Devonian tetrapods more closely. Characters of the dentition provide some of the most useful and illuminating contrasts between sarcopterygians, Devonian tetrapods, and post-Devonian tetrapods.

Premaxillary dentition. The configuration of the premaxillary dentition in the new material, as in the other Devonian forms, and in *Greererpeton*, is apparently derived with respect to related sarcopterygian fishes in the reduction in number of teeth, but primitive with respect to most later tetrapods, in which many forms show a further reduction. Temnospondyls almost invariably retain a large number of premaxillary teeth, usually more than ten, and sometimes as many as eighteen, while reptiliomorphs, microsaurs, aïstopods, lysorophids and nectrideans have fewer. Anthracosauroids usually have fewer than six.

Vomerine dentition. The vomerine dentition of the new material resembles that of *Acanthostega* and osteolepiform and porolepiform fishes rather than most tetrapods, but in possessing an expanded lamina bearing shagreen it may share a derived character with other tetrapods.

Coronoid dentition. No Devonian tetrapod coronoid shows shagreen, and its possession may constitute a derived character uniting post-Devonian tetrapods.

Naris. In the unsutured condition of the premaxillary–maxillary junction, the new material resembles *Acanthostega*, *Ichthyostega* and *Proterogyrinus*. The naris must have been situated low on the snout, and the weight of evidence now strongly suggests that this was the primitive condition, rather than the high position found in *Crassigyrinus*. The low position is found in all three Devonian tetrapods, and in a number of others judged to be primitive on independent grounds, for example *Proterogyrinus* and *Greererpeton*. While the condition in *Crassigyrinus* superficially resembles that of *Eusthenopteron*, it appears to be unusual in structure. It is currently being restudied by one of the authors (J.A.C.). The polarity of this character was debated by Panchen (1985) with respect to judging the validity of outgroup comparisons, but it becomes very hard to argue that a high position as in osteolepiforms and *Crassigyrinus* is genuinely the primitive condition for tetrapods. The question is analogous to that of the condition of the tetrapod stapes, in which strict outgroup comparisons with osteolepiforms suggest that a double-headed stapes should be primitive (Bolt and Lombard 1985). However, single-headed stapes have now been found in three very primitive and unrelated tetrapods, and the weight of evidence (admittedly stratophenetic) strongly suggests that this was really the plesiomorphic condition (Clack 1989, 1992; Bolt and Lombard 1992).

Skull table characters. Among characters of the skull roof bones, those of the tabular show recognizable similarities to those of post-Devonian tetrapods, in particular loxommatids and *Crassigyrinus*, in the presence of a tabular 'horn' or button, and in the form of the paroccipital facet. The tabulars of the other two Devonian forms are each distinctive and apparently specialized. Neither resembles those of sarcopterygian fishes nor other tetrapods. These characters of the new tabulars may constitute synapomorphies with the later tetrapods, at least the so-called 'labyrinthodont' taxa. Similar arguments may apply to the supratemporal, in its proportions and the form of its contacts with other bones.

The apparent occurrence of skulls both with and without a 'kinetic line' between skull table and cheek is of some interest with respect to the polarity of this character. Presence of the 'kinetic line' is usually regarded as primitive (e.g. Watson 1926; Panchen 1970, 1972*b*), and occurs in *Crassigyrinus* and anthracosaurs, but it does not occur in the Devonian tetrapods *Ichthyostega* or *Acanthostega*. A related question is the possession of an intertemporal, whose presence is almost universally regarded as primitive but which is absent in *Acanthostega* and *Ichthyostega*. The significance of these characters is being considered in studies of *Acanthostega* by one of the authors (J.A.C.) and M. I. Coates (University of Cambridge).

Lateral line organs. In having the lateral line organs enclosed in canals through the bone, the new material is fish-like. If the cranial material belonged to one taxon, a greater proportion of the lateral line would have lain in open grooves than in *Acanthostega*, and we should see a condition more like that found in *Greererpeton* (Smithson 1982).

Despite the fact that only two of these cranial elements can be safely attributed to *Tulerpeton*, they supply an important insight into the evolution of certain tetrapod characters, in their divergence from the corresponding sarcopterygian condition. In several characters, these elements most closely resemble those of the contemporary and primitive *Acanthostega* and others more closely resemble those seen in post-Devonian tetrapods. To summarize, in the following characters *Tulerpeton* resembles the other known Devonian tetrapods; in the high number of premaxillary teeth, the vomerine dentition, in lacking shagreen on the coronoid, in the unsutured premaxillary–maxillary junction, and in the low position of the naris. In the following character it resembles post-Devonian tetrapods; in having a shagreen field on the vomer. The postcranial material also shares characters of the radius and ulna, tibia and fibula with post-Devonian tetrapods. The unattributed cranial material shows characters of the tabular, supratemporal and intertemporal shared with post-Devonian tetrapods. The apparent presence of both 'kinetic' and 'unkinetic' skull table forms provides equivocal evidence about the polarity of this character. In the condition of the lateral line canals, the material shows conditions intermediate between the Devonian genera and Lower Carboniferous forms, but it may not all belong to one taxon.

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